The Ohio Naturalist,

and Journal of Science

PUBLISHED BY

The Biological Club of the Ohio State University.

Volume XV. APRIL, 1915. No. 6.

TABLE OF CONTENTS.

THE INHERITANCE OF SIZE IN TOMATOES.*

FRED E. PERRY.

INTRODUCTION AND STATEMENT OF PROBLEM.

Only within the last decade has the attention of students of heredity been turned toward the solution of the problem of the inheritance of quantitative characters. From the very beginning of the science of genetics qualitative characters have been studied until, by means of a series of brilliant discoveries, our knowledge of their inheritance has increased in a wonderful manner. Very little progress has as yet been made, however, in the study of quantitave characters and the inheritance of them has been exceedingly difficult to analyze.

Our present knowledge of heredity has been gained from a microscopical study of the germ-cells, from a statistical examination of data bearing on heredity and from the experimental breeding of plants and animals. The last of the above named methods of studying heredity has been chosen for this work on the inheritance of size in the tomato.

Size is a general term which means the measurement or extent of a thing as compared with something else or with a standard. It is applied to all kinds of dimensions great or small. The volume of a body is equal to the number of cubic centimeters which it contains; it is the amount or measure of tridimensional space. The mass of a body is defined as the quantity of matter

*Contribution from the Botanical Laboratory of the Ohio State University, No. 87.

which it contains. This definition of mass assumes that the quantity of matter is determined by the effect of force upon it. The weight of a body is the force with which the earth attracts that body. It is the measure of the mutual attraction between that body and the earth. The weights of bodies are proportional to their masses at any given place on the surface of the earth.

The tomato fruits are of a very irregular shape as they vary in every degree from a flattened spherical to a nearly perfect spherical, egg, plum or pear-shape. Not only do the various species and varieties differ widely from each other with respect to shape, but there is also considerable variation within the limits of each variety, which fact is especially noticeable when the large, cultivated tomatoes are considered. The large, flattened spherical or cup-shaped tomatoes, like Ponderosa or Livingston's Beauty, are very irregular in shape with many depressions and rounded projections. The long, pear-shaped tomatoes vary especially with respect to length, thickness and breadth of neck. Some fruits have distinct depressions at both stem and distal end while othe fruits have protuberances at these places. A tomato with these protuberances may have the same linear dimensions as a tomato with depressions but yet be of a very different size; or a pear-shaped fruit may have identical linear dimensions with an egg or plum-shaped fruit and yet there be a great size difference. It can thus be readily seen that it is impossible to get a good conception or estimate of the size of a tomato fruit from its linear dimensions.

It is not probable that the specific gravity of the cellular tissue of the fruits varies to any great extent. At least the variation of specific gravity would be reduced to a minimum within a certain definite variety. Since linear dimensions cannot give a true conception of the size of fruit and since there is but little variation probable in the specific gravity of the fruits, it is evident that the weight of a tomato fruit is the best possible index of its size.

Tomatoes are well adapted to the study of inheritance. The cross-breeding of the different varieties and species is comparatively easy and the plants may be readily propogated in a vegetative way. The tomato contains many heritable units, the inheritance of which may be studied. The plants are hardy; they grow without difficulty and mature normal fruit readily under greenhouse conditions.

In spite of the remarkable adaptation of the tomato to work in inheritance of size or weight, no such accurate work has been done with this fruit. A number of men have performed experiments upon the inheritance of the qualitative characters of the plant and fruit. Groth seems to be the only one who has worked with the inheritance of quantitative characters of fruit and he has been studying such characters as the linear dimensions and number of locules. He has taken no weights and from weights alone, it appears to the writer, can accurate data be secured to show the inheritance of size.

This problem in genetics was undertaken with tomatoes because of their remarkable adaptability to work in heredity and because no work had been previously done with them along this line; and it was hoped that some contribution might be made to our scanty store of knowledge regarding the inheritance of quantitative characters—especially the inheritance of size.

MATERIALS AND METHODS USED.

Three crosses were made between pure lines of tomatoes in the greenhouse of the Ohio State University. The first cross was made (1911) between the little red currant tomato, Lycopersicon pimpinellifolium, and the yellow pear tomato, Lycopersicon lycopersicon (Lycopersicon esculentum). In this cross L. pimpinellifolium was used as the staminate parent and L. lycopersicon as the carpellate parent. The reverse cross-pollination was made many times but fertilization never occurred. The second cross was made (1912) between Livingston's Beauty (carpellate parent) and the Yellow Pear (staminate parent). The third cross was made (1914) with Livingston's Beauty as the carpellate parent and Bonnie Best as the staminate parent. It is to be noted that the first cross was made between species while the second and third crosses were made between varieties of L. lycopersicon. All of these pure lines with their hybrids have been growing in the greenhouse and results have been obtained, but completed data is now at hand from only the first cross and this paper will deal almost entirely with results obtained from this hybridization.

These cross-pollinations were made with the utmost care and every precaution was taken to provent the presence of any undesired pollen grains. Two unopened flowers of the same age were selected—each one on a plant of the pure line to be crossed. A capsule of paraffined paper was placed over the staminate bud and both ends were tightly filled with cotton so that the entrance or escape of pollen was absolutely prevented. A tag was attached to the stem of the flower to serve as a means of identification. The sepals, petals and stamens of the carpellate bud were carefully cut away with sterilized pollinating instruments; the stigma was examined with a hand lens to be sure that no pollen grains were present, and the gynecium was capsuled and tagged. After three or four days both capsules were removed and pollen from the stamens of the staminate flower was transferred upon a sterilized glass slide to the stigma of the carpellate flower. Then the pollinated gynecium was capsuled again and left for about a week until fertilization had taken place and the young fruit had begun to enlarge. All the pollinating instruments were carefully sterilized over an alcohol flame, both before and after they were used.

In addition to three crosses above mentioned, a large number of self-pollinations was made according to this method. Of these self-pollinations about 75 were successful. The chances of cross-pollination were small because of the distance between the plants and the absence of insects; but it was considered necessary to have as large a number of self-pollinated fruits as possible to serve as a comparison with other fruits and to furnish pure seed for new cultures of plants.

The soil in which the plants were grown was uniformly of the same composition, as it consisted of two-thirds of greenhouse soil and one-third dry compost. This greenhouse soil was built up after years of experimentation to secure a soil of ideal physical condition for use in pots. The dry compost, which was used, was composed of one-third blue grass sod, one-third leaves and one-third dairy stable cleanings. The greenhouse soil and compost mixed together in the proportions given above, were found to produce a soil ideally adapted, both physically and chemically, to the growth of tomatoes in pots.

The tomato seeds were first planted in a pot of sterilized soil. After the young plants had attained a sufficient size each one was transplanted to a separate two- or three-inch pot. As the plants grew larger they were placed in pots of a greater size until they all came to maturity in the uniform five-inch pots.

These pots were placed from 18 to 24 inches apart in a long row on the benches in the greenhouse. Small bamboo rods about three feet in length were forced horizontally into the soil of the pots and the plants were tied to these supports with raffia. The tops of the upright bamboo rods were fastened with raffia to a long spliced bamboo rod which ran above and parallel to the pots and surface of the bench and which was firmly fastened to upright iron posts that braced the roof of the greenhouse. In this manner ample support was given to the plants even when ladened with fruit.

As soon as the fruits ripened they were gathered and carefully weighed on a pair of accurate balances. A fruit that has been picked for several days will be found to have lost weight by transpiration of water. A ripe fruit that has been allowed to remain on the vine until it has become soft and started to decompose will also give a diminished weight. Every precaution was taken to avoid such diminutions of weight as the fruits were gathered as soon as they became ripe and they were always weighed immediately after they had been gathered.

After each fruit had been weighed the polar length and maximum and minimum equatorial diameters were measured with a pair of calipers. The number of locules was noted and the seeds were carefully counted and saved. The shape and color of fruit were observed. All of this information was carefully recorded in the accession book, together with any unusual features which the fruit may have possessed.

A system of careful labelling was devised and each pot was labelled with an aluminum label by means of which the plant might be identified. The key to the labels was kept in the accession book so that at any time the exact pedigree and descriptions of ancestors of any particular fruit could be readily found. The danger of losing the identity of any plant or fruit was thus reduced to a minimum.

HISTORICAL REVIEW.

Mendel (1860–70) formulated his epoch-making law of heredity as a result of experiments on the inheritance of qualitative characters in garden peas. His results led him to believe that each character depended upon a single determiner or factor, for he worked on simple characters belonging to different parts of the plant. When two plants differing with respect to one unit character were crossed, the segregation in the F-2 generation was computed and found to be in the ratio of 3 to 1. Where there was a difference of two characters between the parents, the F-2 segregation resulted in the ratio of 9 to 7. The possibilities, which would occur when there was a difference of three characters between the parent plants, were computed and the results obtained by breeding came close to the theoretical explanation.

Mendel's law of heredity was rediscovered and rescued from obscurity (about 1900) by De Vries, Correns and Von Tschermak. Following the lead of these three pioneers of heredity, hundreds of other scientists did experimental work along the same lines, until the validity of this law with its three fundamental principles of independence of unit characters, dominance and segregation has been amply proven.

Not until within the last decade, however, was it discovered that the expression of some qualitative characters require the presence of more than a single, separately inherited determiner or factor. Bateson's work in 1908 with two strains of sweet peas (Lathyrus), Bour's investigation with the snapdragon (Antirrhinum) and Castle's experiments with guinea pigs have shown that the qualitative character—color—may depend upon the interaction of at least two gametic factors. East in 1910 (14) found two factors for the production of yellow color in the endosperm of maize. Emerson in 1911 (21) discovered two yellow colors in the endosperm of maize that seemed to be unlike in appearance. Nilsson-Ehle in 1909 (39) crossed a white and browned-glumed wheat and found two factors necessary for the production of the brown-glumed condition, as the F-2 generation segregated into the ratio of 15 brown to 1 white head, which was the expected Mendelian ratio when two factors were required to produce the brown color. When he crossed a red and white-grained wheat, the F-2 generation segregated into the ratio of 63 red to 1 white grain. From this Nilsson-Ehle reasoned that three independent factors were required to produce the red color.

Although the operation of Mendel's law of heredity with respect to qualitative characters has been amply proven, there is a considerable doubt in the minds of many foremost geneticists as to whether or not quantitative characters are inherited in a Mendelian fashion. It has only been within the last few years that students of heredity have turned their attention to the problem of inheritance of quantitative characters.

The first man who worked definitely with quantitative characters seems to have been Lock in 1906 (36) who crossed a tall race of maize with a shorter race and obtained an F-1 hybrid intermediate in size between the parents. The F-2 plants showed no segregation when crossed with one of the parents. Lock showed that the height of a plant is not inherited in a simple Mendelian fashion.

Castle in 1909 (8) worked with the ear-lengths of rabbits and discovered what he called "blending inheritance". In summing up his own work Castle says, "A cross between rabbits differing in ear-lengths produces an off-spring with ears of intermediate length, varying about the mean of the parental ear-lengths. * * * * A study * * * * shows the blend of parental characters to be permanent. No reappearance of the grand-parental ear-lengths occurs in the F-2 generation, nor are the individuals of the second generation as a rule more variable than those of the first generation of cross-breeds. * * * * The linear dimensions of the skeletal parts of an individual approximate closely the mid-parental dimensions".

Ghigi in 1909 (22) crossed a Paduan fowl and a bantam and found that the size of body and eggs of the F-1 cross-bred individuals were intermediate between the parent races. Only a limited number of the later generations were grown and these showed no segregation of size characters.

Mendelians have not recognized the validity of any so-called "blending inheritance" except that which Castle has shown. And these results on the ear-lengths of rabbits have been explained according to the Mendelian notation by Lang, whose explanation is recognized as possible by Castle. Some Mendelians object to this "blending inheritance" on the grounds that the number of individuals grown was not large enough to prove that segregation does not occur in the F-2 generation and Castle has admitted the possibility of this fact.

The experiments of Phillips in 1912 (40) upon the inheritance of size in ducks were more extensive than the work of Castle or Ghigi. He crossed a Mallard with a Rouen duck and found that the F-1 birds were intermediate in size as compared with the parents. Segregation was present in the F-2 generation. Phillips concludes, "The amplitude of variation of the F-2 fowls is greater than that of the F-1 fowls but does not extend beyond the nearer limit of the respective grandparental races."

Nilsson-Ehle (1908) showed how the Mendelian notation for the inheritance of qualitative characters might be used as a basis for the explanation of the inheritance of quantitative characters.

East in 1910 (14) in ignorance of Nilsson-Ehle's 1908 paper, developed a similar theory and showed how certain data on the inheritance of the number of rows of grains on an ear of maize could thus be analyzed.

Emerson in 1910 (19) issued a paper on the inheritance of quantitative characters in Cucurbita pepo, Phaseolus vulgaris and Zea mays. He showed segregation of size factors but offered no Mendelian explanation.

Johannsen (32) crossed two lines of beans and worked with the inheritance of length and breadth. He found the F-1 generation intermediate between the parent biotypes. The F-1 beans were no more variable than the parents but no definite conclusions can be drawn from this fact as only a limited number were grown. The F-2 and F-3 generations showed greatly increased variability over that of the parent biotypes. The length of the parent beans differed widely from each other. Neither the F-1 nor F-2 generation reached the extremes in length of the parent biotypes but the F-3 generation did reach those extremes. The breadth of the parent beans were very similar. The F-2 generation exceeded in breadth the extremes of the parent biotypes, while the F-3 generation more widely overlapped those extremes.

Belling in 1912 (1 and 2) crossed two widely different bean varieties. The F-1 generation exceeded in size of seed and plant either of the parents. The F-2 generation showed marked variability.

East in 1913 (13) worked upon the corolla length of Nicotiana and found the F-1 hybrid corolla length to be the geometrical mean between the parent lengths. The F-2 generation showed greater variability than the F-1 generation.

Groth in 1912–13 (26, 27, 28 and 29) conducted extensive experiments upon the inheritance of tomato seedlings, leaves and fruits. He worked with linear dimensions and found the F-1 fruit to be the geometrical mean between the parental dimensions. Marked segregation of size occurred in the F-2 generation. His Mendelian explanation of the results is very complicated and will be discussed later in this paper.

Punnet in 1914 (44) conducted extensive experiments upon the inheritance of weight in poultry. He obtained an F-1 bird intermediate in size between the parents while the F-2 generation showed strong segregation. These experiments are still in progress. His latest report (February, 1914), says that the work is not yet advanced far enough to permit of complete analysis, "but the nature of the F-2 generation raised last year strongly suggests that size depends upon definite factors which exhibit ordinary Mendelian segregation."

In addition to the experiments above noted, other work of like nature has been done within the last few years. No definite results regarding the explanation of the inheritance of quantitative characters have as yet been obtained. Castle says (6) (March, 1914), "Although extensive observations upon the subject of size inheritance in both animals and plants have been made, they have resulted in the demonstration, as yet, of no single clear-cut Mendelizing unit character (or factor either)."

INFLUENCE OF ENVIRONMENTAL CONDITIONS.

The influence of environment in the present series of experiments may be considered under four heads.

LIGHT. The growth of the plants was influenced not only by the intensity but by the duration of light. In the tomato plants, as in other species, assimilation commences with a certain minimum and increases as the intensity of the light rises until a certain optimum is obtained.

Light that is too strong is injurious. The period of ripening of the fruits was shortened in proportion as the optimum light intensity was reached. In the winter when both the intensity and duration were low the plants ceased to bloom but produced normal fruits as long as they did bloom. There is no evidence to show that the light conditions present in the greenhouse in any way influenced the size of fruit.

TEMPERATURE. According to Warming (b), "Each of the various vital phenomena of plant-life takes place only within definite (minimum and maximum) limits of temperature, and most actively at certain (optimum) temperature; these temperatures may even differ in respect to the different functions of one species." From this it may be inferred that the lower greenhouse temperatures in winter may have had some influence in causing the tomato plants to cease to bloom, since the lower critical limits for reproduction, as with many other species of plants, is evidently higher than that required for growth. The various temperatures of the greenhouse (45° to 100° F.) came within the cardinal points for growth and, as far as could be ascertained, seemed to have no appreciable influence upon the size of the fruits.

(b) See (40) page 22.

MOISTURE. The noticeable lack of moisture will cause a plant to become ill-nourished and dwarfed. The moisture conditions in the greenhouse were controlled as perfectly as possible and the tomato plants were watered quite often, but even then optimum moisture conditions did not prevail. The lack of a constant abundance of water probably exerted a great limiting influence upon the size of plant. The transpiration of water is directly proportional to the amount of leaf surface and, after the plant has reached a certain mature size, the leaf surface becomes limited as the amount of moisture in the pots is limited. The plants grown in the garden attained a greater size than the potted plants and one of the principal reasons for this difference was the more constant and abundant supply of soil-water present in the garden environment. There was no corresponding influence upon the size of fruit, as there was no noticeable difference of fruit-size as a result of the different moisture conditions under which the plants were grown.

SOIL. The quantity and quality of the essential nutritive substances in the soil, as well as the physical condition, influences the size of a plant and fruit. Warming says (b), "Defective nutriment (that is an inadequate supply of one or more substances) may be the cause of dwarf-growth (nanism); this has been demonstrated by many physiological investigations." All of the potted plants in these experiments were supplied with a soil as perfectly adapted as possible, both physically and chemically, to the growth of the tomato. And yet, the amount of available plant nutriment in a five-inch pot is necessarily somewhat limited while the available nutriment substances are more abundant in the garden, so that this lack of nutriment in the pots together with the lack of perfect moisture apparently caused the difference in size between the greenhouse and garden-grown plants. There was not enough difference, however, between the soil and moisture conditions of the greenhouse and the garden to cause any appreciable change of fruit-size.

Two experiments were tried to determine the effect of different kinds of soil conditions upon the size of plant and fruit.

The first experiment was performed in order to show the effect of the garden conditions upon the size of plant as compared with the effect of the greenhouse environment upon the size of the same plant. In the garden the soil contained more available nutriment and moisture than were present in the pots. A number of plants of the F-1 generation (17–12–2) were grown in the greenhouse where they attained at full maturity a height of about 2.5 feet and a diameter of 1.5 feet. One of these plants was afterwards removed to the garden where it grew to be 3 feet high and covered

(b) See (40) page 56.

a circular space of ground about 10 feet in diameter. Unfortunately no fruits were weighed while the plant was grown in the greenhouse, but any increase in the size of fruit, as a result of the garden conditions, was so slight as not to be apparent.

The second experiment was completed in order to determine the effect of a soil which contained very little plant nutriment that was available, upon the size of plant and fruit. Plant 10 of the F-3 generation (17–12–4) grew in the greenhouse to be about 7 feet tall and possessed an average fruit of 2.22 grams. A cutting of this plant was grown in an eight-inch pot filled with pure, washed, desert sand which contained very little plant nutriment. An inch layer of normal pot-soil was added in the middle of the pot as it was feared the scarcity of nutriment would cause the plant to die before it reached maturity. The light temperature and moisture conditions were identical with both plant 10 and the cutting. The plant in the sand grew to be only 21 inches high and its average fruit weight was found to be .85 grams. The size of plant and fruit were reduced 75% and 61% respectively. This shows the effect of extreme lack of the essential nutritive substances upon the size of the plant and fruit.

In addition to the F-1 plant grown in the garden, as described in the first experiment, a number of other plants of the parental and hybrid generations of this currant-pear cross has been grown both outside and inside the greenhouse. Any effect upon the fruit, as a result of greenhouse environment, would probably be shown by a decrease in size. So far as can be ascertained, however, from all the evidence now at hand, there was no appreciable difference in the size of fruits as a result of the different environmental conditions of the greenhouse and garden.

Even if there were a small diminution in the size of the tomato fruit as a result of being grown in the greenhouse, this change of size would affect all plants in the same way and in the same proportion, and, as all the plants concerned in this problem are greenhouse grown, the accuracy of the ratio between the sizes of the parents and offsprings, which is the vital part of the thesis, would remain unimpaired.

The average weight of the first ten fruits of a plant was compared with the average weight of ten fruits taken in the latter part of the fruit bearing period. A number of plants were examined in this manner and it was found that the fruits which ripened first were not larger than those which ripened later, nor was any correlation discovered between the size and time of blooming. The relation between the time of blooming and the size of fruit on a single cluster was examined and considerable data collected but no correlation was found to exist.

FLUCTUATING VARIATIONS.

Any quantitative character is subject to deviation from the average condition. According to the laws of chance these deviations are sometimes plus and sometimes they are minus, as a result of which they have been termed "fluctuating variations". Quetelet has shown that all living structures vary and are always grouped about a mean. In other words plus or minus deviations of increasing magnitude occur with diminishing frequency in such a way that a given population will be distributed, in a large part, at or near this mean or mode. Galton called attention to this

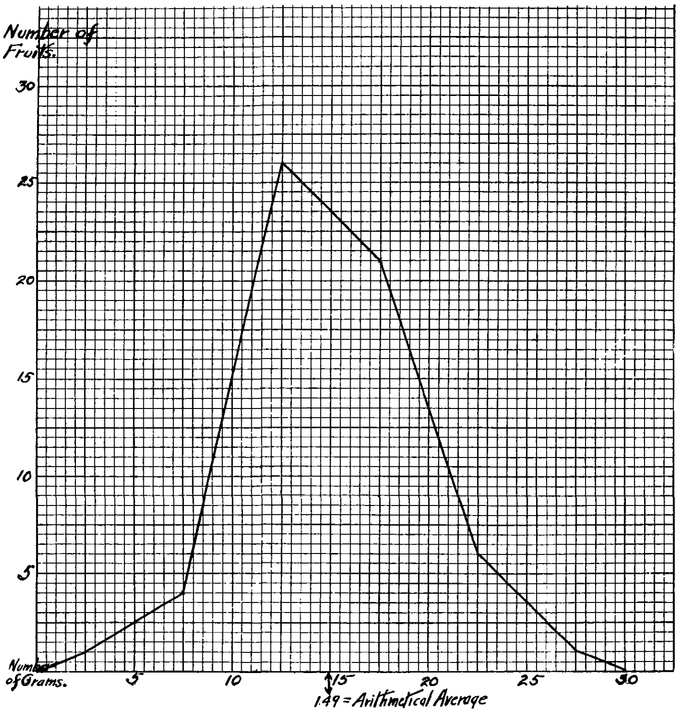


Figure 1

same fact in another way when he stated that the offspring of parents with plus or minus variations are closer to the average than the parents. There are always certain limits of fluctuating variability beyond which the deviations do not extend.

Since the fruit of the individual plants were found to be subject to these fluctuating variations in size, it was considered necessary to harvest a large number of fruits from two typical plants in order to determine both the nature and degree of such variations. From plant 7 of the series 17–12–4 (F-3 generation) 58 fruits were examined. The curve formed by these weights is shown in Figure 1. The fruit-weights vary 2.35 grams. The mode is shown to be less than the arithmetical mean and therefore the skew is negative.

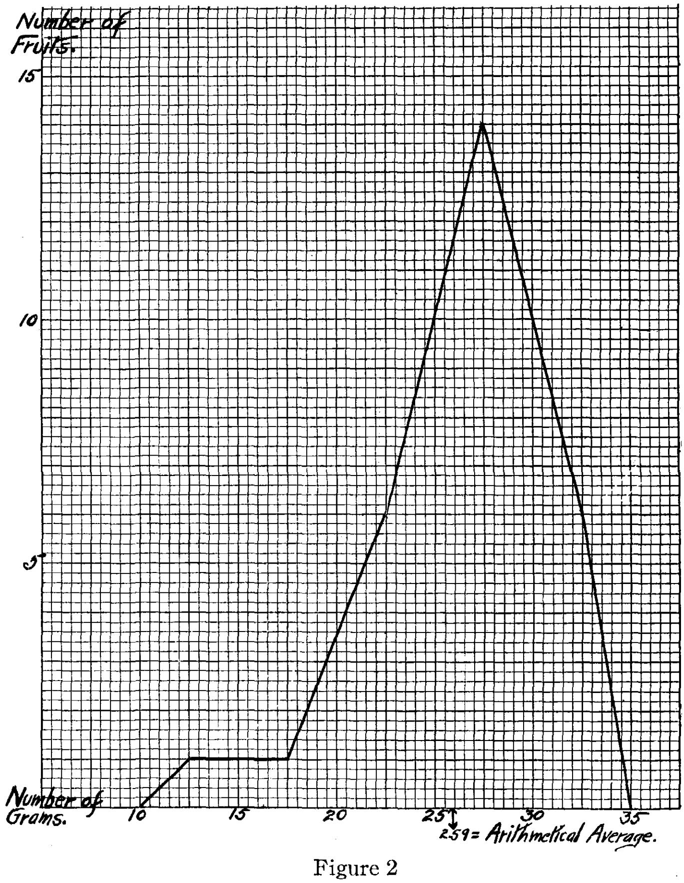


Figure 2

From plant 14 of the series 15–11–2—II–II (F-2 generation) 28 fruits were harvested and the curve formed by the weights of these fruits is shown in Figure 2. The fruit-weights vary 1.93 grams. As shown on this plate the mode is a little more than the arithmetical mean and therefore the skew is slightly positive.

The ideal plant fruit-size would have been obtained if it had been possible to harvest from each plant 1000 fruits or more and the modal average taken. As this could not be done, it was determined to select at least ten representative fruits from a plant, the arithmetical average of which would be considered the average fruit-size for that plant. In some cases, however, it was not possible to harvest at least ten fruits so that a few plants are represented by only four or five to nine recorded fruits. In the selection of the fruits to be gathered the greatest degree of care and accuracy was observed. One of the largest and one of the smallest fruits were first taken, after which the remaining fruits were selected as near to the mode of the fruit size as possible. It is believed that the deviation of the recorded fruit-weight of any plant, based on ten selected fruits, does not vary more than plus or minus .2 gram from the actual fruit-weight which would have been secured had all the normal fruits of that plant been harvested. But even if the error of plant fruit-size were twice that amount it would not materially affect the results of this work.

RESULTS OBTAINED.

The plants of the Yellow Pear tomato (carpellate parent) possessed the following average fruit-weights:

2-11-16.	Plant	2	=	19.26	grams.
"	"	3	=	17.84	"
"	"	4	=	12.71	"
"	"	5	=	17.84	"

The average fruit-weight of this parent pure line is 16.91 grams.

The variability of the average fruit-sizes of the plants of the Red Currant tomato (staminate parent) is very slight and fruits from only two plants were weighed. The following average fruit-weights were obtained from these plants:

7-11-2.	Plant	1	=	.66	gram.
"	"	2	=	.62	"

The average fruit-weight of this parent pure line is .64 gram.

The F-1 hybrid generation of this cross was found to be intermediate in size. The plants possessed the following average fruit-weights:

17-12-2.	Plant	1	=	1.90	grams.
"	"	2	=	2.48	"
"	"	3	=	2.22	"
"	"	4	=	3.46	"
"	"	5	=	3.76	"

The F-1 generation average is 2.76 grams. The geometrical mean between the weights of the parents is 3.28 grams which is only .52 gram more than the actual arithmetical mean of the fruit-weights. It is to be also noted that two F-1 fruits are heavier than 3.28 grams while three fruits are lighter. There is thus a remarkable agreement between the geometrical mean and the actual generation fruit average.

There were four distinct series of F-2 plants grown. Each series was derived from a separate parent F-1 plant or fruit. The following table shows the average fruit-weights of the plants of the F-2 series 15–11–2—II–I:

15-11-2—II-I.	Plant	1	= 2.56	grams.
"	"	2	= 2.48	"
"	"	4	= 3.06	"
"	"	5	= 1.49	"
"	"	7	= 1.48	"
"	"	8	= 2.28	"
"	"	9	= 1.86	"
"	"	10	= 3.18	"
"	"	11	= 4.16	"
"	"	12	= 2.55	"

The average weight of fruit for the above series is 2.54 grams.

The series 15–11–2—II–II, was composed of F-2 plants which gave the following average weights of fruits:

15-11-2—II-II.	Plant	1	= 1.43	grams.
"	"	3	= 1.99	"
"	"	4	= 1.89	"
"	"	5	= 1.94	"
"	"	6	= 3.42	"
"	"	7	= 1.53	"
"	"	8	= 1.56	"
"	"	9	= 3.34	"
"	"	10	= 3.80	"
"	"	11	= 2.00	"
"	"	12	= 1.69	"
"	"	14	= 2.69	"
"	"	15	= 2.42	"
"	"	17	= 2.60	"
"	"	18	= 2.25	"
"	"	19	= 2.61	"
"	"	20	= 1.33	"
"	"	21	= 2.87	"

The average weight of fruit of this series is 2.29 grams.

The following table shows the average fruit-weights of plants of the F-2 series 15–11–2—5–1:

15-11-2—5-1.	Plant	1	= 3.39	grams.
"	"	2	= 2.36	"
"	"	3	= 3.30	"
"	"	4	= 2.11	"
"	"	6	= 2.67	"
"	"	7	= 2.86	"
"	"	8	= 3.83	"
"	"	9	= 1.36	"
"	"	10	= 2.36	"
"	"	11	= 1.87	"
"	"	12	= 1.88	"

The average weight of fruits of this series is 2.54 grams.

The fruits of the F-2 series 15–11–2 gave the following average weights of fruits:

15-11-2.	Plant	1	=	2.36	grams.
"	"	3	=	1.76	"
"	"	5	=	3.60	"
"	"	6	=	2.16	"
"	"	7	=	3.00	"

The average weight of fruits of this series is 2.58 grams.

These four series of F-2 generation hybrids give a total of 44 F-2 plants whose average fruit-weights vary from 1.33 grams to 4.16 grams. The lightest fruit possessed a weight of .38 gram while the heaviest fruit weighed 5.63 grams. The variability of the F-2 fruits was greater than that of the F-1 fruits. The average fruit-size of the F-2 generation plants agrees fairly well with the average of the fruit-size of the parent F-1 generation. Distinct segregation of size characters was noted in the F-2 fruits.

The following table shows the average fruit-weights of the plants of the F-3 generation (17–12–4):

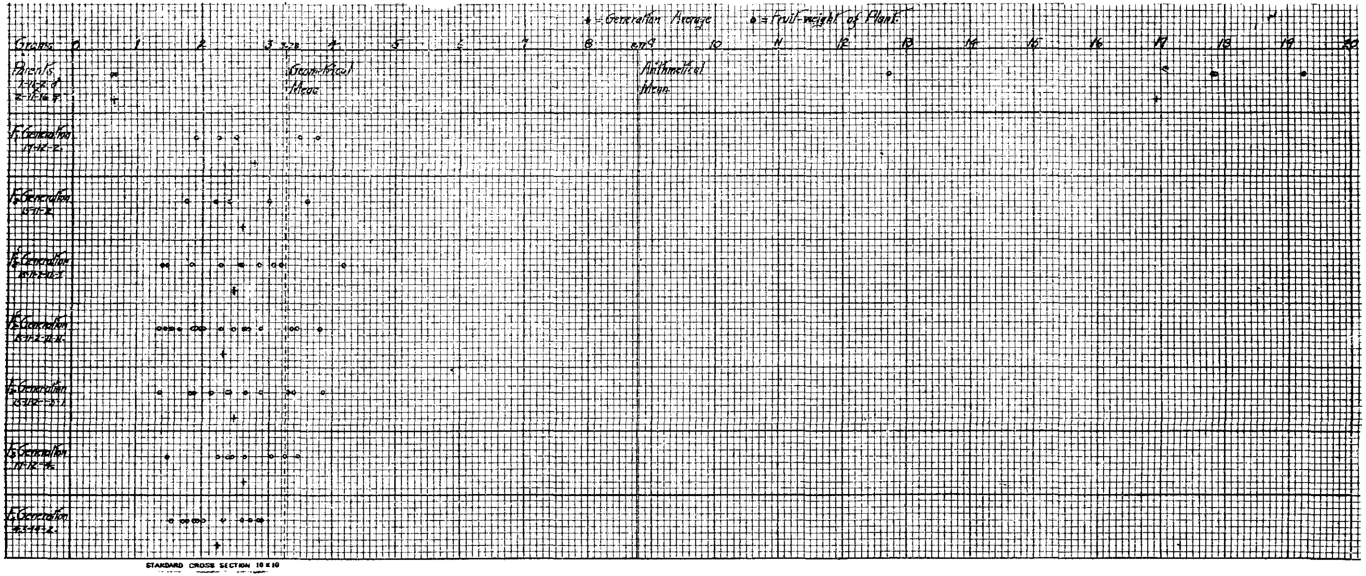
17-12-4.	Plant	1	=	3.25	grams.
"	"	4	=	2.40	"
"	"	5	=	2.42	"
"	"	6	=	3.06	"
"	"	7	=	1.50	"
"	"	8	=	3.46	"
"	"	9	=	2.62	"
"	"	10	=	2.22	"

In this generation segregation of size characters of fruit was observed. The average weight of fruit for this generation was found to be 2.62 grams. The variability and generation average are practically the same as in the F-2 fruits.

From plant 10 of the F-3 series came the seeds which produced the plants of the F-4 generation (43–14–2). This generation was grown in the garden. The average fruit weights of the different plants are as follows:

43-14-2.	Plant	1	=	2.30	grams.
"	"	2	=	2.73	"
"	"	3	=	1.94	"
"	"	4	=	1.95	"
"	"	5	=	1.80	"
"	"	6	=	1.74	"
"	"	7	=	2.87	"
"	"	8	=	1.56	"
"	"	9	=	2.03	"
"	"	10	=	2.59	"
"	"	11	=	2.85	"

Segregation of size characters of fruit occurred in this F-4 generation. Both variability and the average size of fruit of the generation are somewhat less than in the F-3 fruits.



PERRY on "The Inheritance of Size in Tomatoes."

The average weight of fruit the F-3 parent, plant 10, is 2.22 grams while the F-4 generation possessed an average fruit-weight of 2.215 grams—a remarkable similarity between weight of parent fruit and the average weight of fruit of offspring. It is further to be noted that six fruits are lighter and five fruits are heavier than 2.22 grams, so that there is as equal a variation as fruit-size as possible in the offspring on each side of this parental fruit-weight. This relation between parent and offspring is graphically shown on Plate XXII.

Over 700 fruits were harvested from 74 plants in this series of experiments. This data is summed up and the relationship between the parental and hybrid fruit-weights is shown on Plate XXII.

INTERPRETATION OF RESULTS.

When the results, which were obtained, are interpreted it should be clearly kept in mind that the recorded weights represent the average fruit-weight of a single plant and not the weight of a single fruit. In practically all of the known experiments along this line the individual fruit-weights have been used as a basis for study and these weights have been shown in the tables of results. There is no evidence to show, in a number of experiments, at least, that any special care was observed in the selection of fruits, which seemed to be taken at random from a hybrid generation or a pure line of plants. The fluctuation in size of fruit on each plant; the difference in the number of fruits produced on each plant; and the variation in the length of the fruit-bearing period render the results secured by such harvesting liable to considerable error. On the other hand, when an accurate record is kept of each fruit and the average fruit-weight of each plant, more accurate results (especially the generation average based on the fruit-weight of the plants) are bound to be obtained.

There are only a few recorded experiments which deal comprehensively with the subject of the inheritance of size of fruit in the F-1 generation. This scarcity of data, taken together with its complexity, render the correct analysis of this problem very difficult. Especially has there been a great deal of discussion among scientific men as to whether the F-1 fruit-sizes approach more nearly to the geometrical or to the arithmetical mean between the parent sizes.

Groth, basing his statement upon linear dimensions, reports that the size of the F-1 tomato fruits is the geometric means between the parents. In this view he is supported by Bruce who had previously obtained like results with tomatoes. The data presented in this paper also shows that the F-1 fruits of the tomato (currant-pear cross) are the geometric means between the parental sizes.

Emerson says (b), "A hurried examination of data, both published and unpublished, derived from my own studies of size in beans and maize, indicates that the F-1 sizes are nearer the average than the geometric means between the parent sizes." When all of the available data of Emerson is considered, a part of the F-1 sizes show a near approach to the geometric mean and a part to the average. He made a cross between the Black Mexican and Tom Thumb varieties of corn and obtained an F-1 hybrid whose weight was the exact geometric means between the parent weights. The breadth of the hybrid seeds, however, show a closer approach to the arithmetical than to the geometrical mean.

A very extensive series of experiments have been conducted at the New Jersey Experiment Station upon the quantitative inheritance of characters in peppers. Part of the F-1 sizes approach the arithmetical and part approach the geometrical mean between the parents.

From the data enumerated above and from the other available data, it appears that there has not as yet been a sufficient amount of work done to enable a definite statement to be made, as to whether the F-1 fruits approach more nearly the arithmetical than the geometrical mean between the parental sizes. Neither is it certain that all the F-1 fruit-sizes can be made to approach more nearly to one than to the other of these two means. The suggestion came to the mind of the writer of this paper that perhaps there was some correlation between the relative difference of parental fruit-sizes and the approach of the F-1 fruit-size to the geometrical or arithmetical means between these parents. Accordingly all available data upon F-1 size inheritance was studied. This examination seemed to indicate that when two varieties are crossed which differ greatly in fruit-size (the fruit-size of one parent being probably about two, three or more times the size of fruit of the other parent), the resulting F-1 fruit-size will be nearer to the geometrical than the arithmetical mean; but when two parents similar in fruit-size are crossed, the size of fruit of the F-1 offspring will approach more nearly to the arithmetical than the geometrical mean. There are some exceptions to this statement but as a general rule it was found to be true. This statement has been formulated not because it is well understood but because it may suggest principles of size inheritance which lie deeper than those now known and which, it is hoped, will be more fully known in the light of future investigations.

The inheritance of size of fruit in the F-2 generation has received even less study than the inheritance of size in the F-1 generation. Groth seems to have been the only one to attempt an explanation. He has worked out a theoretical hypothesis,

(b) See (20) page 57.

based on linear dimensions, to show complete segregation of size characters, varying in the Mendelian fashion from the larger to the smaller parent. He assumes a cross between two tomatoes with the linear dimensions 4x4x4 and 9x9x9 respectively, and gets an F-1 hybrid which is 6x6x6. He assumes factors for length, width, breadth and shape. Shape modifies the dimensional factors, while each of the three dimensional factors modifies the other two, from which it can be seen that this is a multiple factor hypothesis. If all the tomato fruits were perfect spheres, this explanation would be more tenable; but, as noted before, the extreme irregularity of shape causes any explanation, founded on linear dimensions, to be liable to considerable error.

The results presented in this paper, showing apparently such unusual dominance of the red currant size factors, cannot be interpreted by Groth's hypothesis. However, a Mendelian explanation has been worked out which agrees fairly well with the facts. This explanation is given in the following paragraph, as it seems to be the best possible interpretation of these results at the present time.

As noted before, Nilsson-Ehle in his work on tri-hybrid red wheat found in the second generation 63 grains of varying redness to one white wheat grain. From this he reasoned that the red grains possessed three independent color factors each of which was able to give the red color to the wheat. In the F-2 tomato generation 44 plants have been grown and the segregation of size characters has been so incomplete as to warrant the assumption of at least four size factors. The small size factors of the red currant seem to be incompletely dominant over the large size factors of the yellow pear, because, when an equal number of large and small size factors are present, as in the F-1 generation, the geometrical mean between the parents is realized. As the number of small size factors increases or decreases from the number present in the F-1 generation so will the weight of the resulting fruit vary more or less from the geometrical mean. This variation will not be large, as the small size factors, however few, are incompletely dominant over any number of large size factors. There should be occasional returns to both parent sizes, the frequency depending upon the number of factors concerned. If, with further experiments, no such original parental size is ever attained, there is evidently more than multiple factors involved.

SUMMARY.

1. A more accurate representation of the size of tomato fruits can be obtained from their weights than from their linear dimensions.

2. The size of fruit of the F-1 generation of the currant-pear cross is the geometrical mean between the parental sizes.

3. From an examination of all available data upon the inheritance of fruit-size in the F-1 generation, it appears that, when two varieties are crossed which differ widely in fruit-size (the size of fruit of one parent being probably about two, three or more times the size of fruit of the other parent), the F-1 fruit-size will be nearer to the geometrical than the arithmetical mean; but, when two parents similar in fruit-size are crossed, the size of fruits of the offspring will approach more nearly to the arithmetical than to the geometrical mean.

4. The average fruit-size of the F-2 generation does not exceed and is even slightly less than the average fruit-size of the F-1 generation. The segregation of size factors and the incomplete dominance of the small size factors of the red currant parent may be explained by the assumption of at least four size factors. If no parental sizes can be ever obtained, there may be more than multiple factors involved.

5. The fruits of the F-2 and F-3 generations agree fairly well with respect to variability and average generation size. The F-4 fruits show diminished variability and size.

6. This paper deals only with the inheritance of size in the currant-pear tomato cross. Conclusions as to how far the results obtained may be applied to the inheritance of size in crosses between other species and varieties must be left to the accumulation of further data.

1. BELLING, JOHN. Velvet Beans crossed with Lyon Beans. Ann. Rpt. Florida Agr. Exp. Sta. 1910: 79-92.
2. .... Second Generation of the Cross between Velvet and Lyon Beans. Ann. Rpt. Florida Agr. Exp. Sta. 1911: 82-103.
3. BRUCE, A. B. The Golden Mean. Science N. S. 40: 59.
4. .... Heredite des caraters quantitatifs, (4 Conf.-int. Genetique Paris 1911 4pp.)
5. CASTLE, W. E. Heredity in Relation to Evolution and Animal Breeding. 1911.
6. .... Pure Lines and Selection. Jour. Hered. Vol. 5. 1914.
7. .... The Inconstancy of Unit Characters. Amer. Nat. 46: 352-362. 1912.
8. .... Studies of Inheritance in Rabbits. Car. Inst. Wash. Pub. 114: 5-70. 1909.
9. COLLINS, G. N. The Value of First Generation Hybrids in Corn. Bu. P. Ind. 191. 1910.
10. DE VRIES, HUGO. Plant Breeding. 1907.
11. .... The Principles of the Theory of Mutation. Science. N. S. 40: 74-88. 1914.
12. East, E. M. The Genotype Hypothesis and Hybridization. Am. Nat. 45: 160-174. 1911.
13. .... Inheritance of Flower Size in Crosses between Species of Nicotiana. Bot. Gaz. 55. 1913.
14. .... A Mendelian Interpretation of Variation that is Apparently Continuous. Am. Nat. 44: 65-82. 1910.
15. EAST, E. M. and HAYES, H. K. Inheritance in Maize. Con. Agr. Exp. Sta. 167.

16. EMERSON, R. A. Inheritance of the Ligule and Auricles of Corn Leaves. Ann. Rpt. Nebraska Agr. Exp. Sta. 25: 81-88. 1912.
17. .... Genetic Correlation and Spurious Allelomorphism in Maize. Ann. Rpt. Neb. Agr. Exp. Sta. 24: 60-90. 1011.
18. .... The Inheritance of a Recurring Somatic Variation in Varigated Ears of Maize. Neb. Agr. Exp. Sta. Res. 4. 1913.
19. .... Inheritance of Sizes and Shapes in Plants. Amer. Nat. 44: 739-746. 1910.
20. .... Multiple Factors vs. "Golden Mean" in Size. Inheritance. Science N. S. 40: 52-59. 1914.
21. EMERSON, R. A. and EAST, E. M. Inheritance of Quantitative Characters in Maize. Neb. Agr. Exp. Sta. Res. 2. 1913.
22. GHIGI, ALESSANDRO. Ricerche di sistematica sperimentali sul genere Gennaeus wagler. Bologna p. 38. 1909.
23. GILBERT, ARTHUR W. A. Mendelian Study of Tomatoes. Am. Breed. Assn. Mag. 7: 169-188. 1912.
24. GORD, M. Hybrides binaires de premiere generation dans le genere Cistus et. caracters Mendeliens. C. R. Ac. Sc. Paris. C. L. p. 239. 1910.
26. GROTH, B. H. A. The "Golden Mean" in the Inheritance of Size. Science N. S. 39: 581-584. 1914.
27. .... The F-1 Heredity of Size, Shape and Number in Tomato Fruits. New Jersey Agr. Exp. Sta. 242. 1912.
28. .... The F-1 Heredity of Size and Number in Tomato Seedlings. New Jersey Agr. Exp. Sta. 238. 1911.
29. .... The F-1 Heredity of Size and Number in Tomato Leaves. New Jersey Agr. Expo. 239. 1911.
30. HALSTEAD, BRYON D. Experiments with Peppers. Thirty-Fourth Ann. Rpt. New Jersey State Agr. Sta. 1913.
31. HAYES, H. K. Correlation and Inheritance in Nicotiana Tobacum. Connecticut Agr. Exp. Sta. 1913.
32. JOHANNSEN, W. Elemente der Exakten Erblichkeitslehre.
33. .... Genotype Conception of Heredity. Amer. Nat. 45: 129-159. 1911.
34. KEARNEY, T. H. Mutation in Egyptian Cotton. Jour. Agr. Res. 2: 287-302. 1914.
35. LITTLE, C. G. A Possible Mendelian Explanation for a Type of Inheritance Apparently Non-Mendelian in Nature. Science N. S. 40: 904-906. 1914.
36. LOCK, R. H. Studies in Plant Breeding in the Tropics. III. Experiments with Maize. Ann. Roy. Bot. Gard. Perademja. 3: 95-184.
37. MACDOWELL, E. C. Multiple Factors and Mendelian Inheritance. Jour. Exp. Zool. 16: 177-194. 1914.
38. MUMFORD, F. B. Influence of Size of Parent on Birth Weight. Am. Breed. Assn. Mag. 1: 73-76. 1906.
39. NILSSON-EHLE, H. Uber enstchung scharf abweichender Merkmale aus Kreuzung gleichartiger Formen bein weizen. Berichte der Deutschen Botanischen Gesellschaft Band. XXIX. Heft 2, 1911. Marz.
40. PHILLIPS, JOHN C. Size Inheritance in Ducks. Jour. Exp. Zool. 12: 369-380. 1912.
41. PRICE, H. L. and DRINKARD, A. W. JR. Inheritance in Tomato Hybrids. Pl. World 12: 10-18. 1909.
42. ....Inheritance in Tomato Hybrids. Virginia Agr. Exp. Sta. 177. 1908.
43. PUNNET, R. C. Mendelism in Great Britain. Jour. Hered. 2. 1914.
44. .... Inheritance of Weight in Poultry. Jour. Gen. 4: 23-40. 1914.

EXPLANATION OF PLATES.

Plate XXIII.

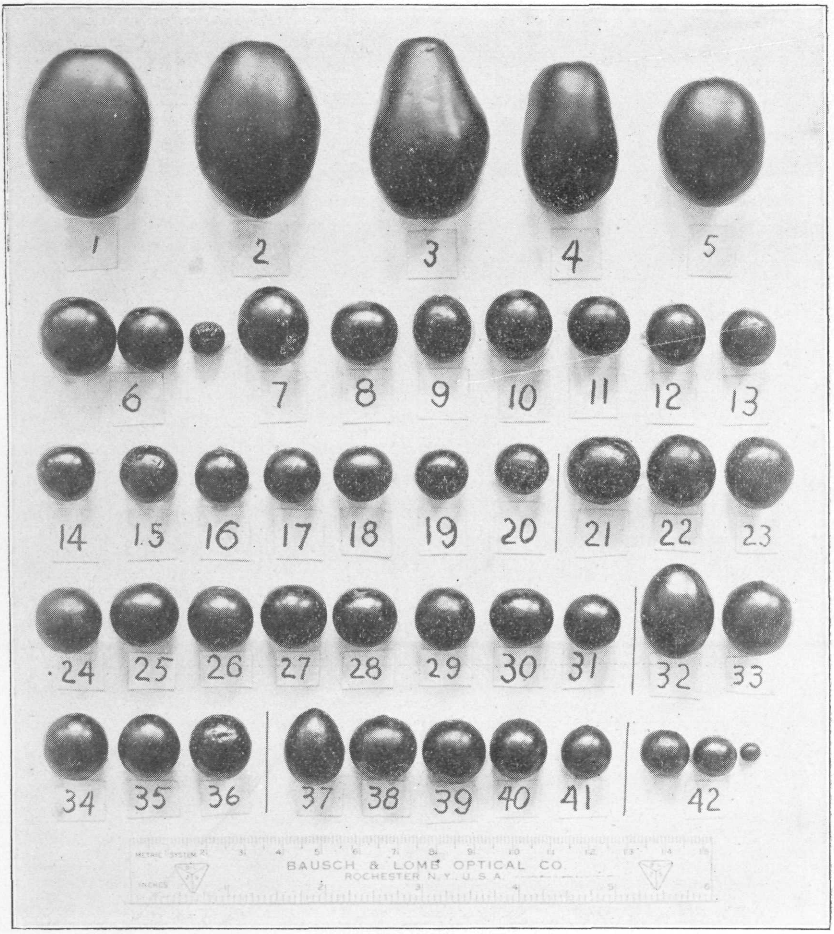
The different sizes of parent and hybrid fruits shown in this plate were photographed July 27, 1914, and the fruits were gathered and weighed two days before that date. It was not possible to show all of the different sizes and shapes of fruits as all the plants did not mature at the same time. One typical fruit was selected from each plant. In addition to the data given below the number of seeds of each fruit can be fcund in the records. The identity of the fruits is as follows:

NO. OF FRUITS.	FRUIT TAKEN FROM	WEIGHT IN GRAMS.	POLAR LENGTH MAX. DIAMETER, MIN. DIAMETER.	COLOR, SHAPE AND NO.OF LOCULES.
1	2-11-16. plant 3	21.04	41.5x32.5x28.7	yel., plum, 2
2	" " 5	20.02	43. x31. x29.	" " 2
3	" " 3	18.87	40.6x30.4x28.	" pear, 2
4	" " 5	13.13	37.2x25.1x24.1	" " 2
5	" " 4	12.69	32.1x26.8x24.4	" plum, 2
6	max. 17-12-4. plant 4	4.00	19.7x19.7x18.	red, sph. 2
6	av. " " 2	2.43	16.5x16.5x16.	" " 2
6	min. " " 2	.49	9.2x x	" " 2
7	15-11-2-II-II. plant 6	3.35	20. x18.1x16.8	" plum, 2
8	" " 19	2.45	16.2x17. x15.7	" sph. 2
9	" " 17	2.62	17.8x14. x14.	" egg, 2
10	" " 21	2.80	17.6x17.1x16.4	yel. sph. 2
11	" " 15	2.06	15. x15. x14.8	red, " 2
12	" " 4	2.29	15.9x14.9x14.3	" " 2
13	" " 3	1.91	15.1x14.1x13.8	" " 2
14	" " 7	1.79	14. x14.8x14.3	" " 2
15	" " 5	2.01	14.7x15.1x14.2	yel. " 2
16	" " 18	1.26	15.2x13.8x15.3	red, " 2
17	" " 14	1.61	14. x14.5x14.	yel. " 2
18	" " 1	1.76	13.9x15. x13.9	" " 2
19	" " 11	1.34	12.8x13.9x13.1	" " 2
20	" " 20	1.41	13.4x14.3x13.7	" " 2
21	15-11-2-II-I. " 10	3.37	17.2x18.2x17.7	" " 2
22	" " 2	3.22	18.7x17.6x16.6	red, " 2
23	" " 11	3.21	18.7x17.8x17.1	" " 2
24	" " 1	2.98	16.9x17.3x16.4	" " 2
25	" " 10	2.84	16.4x17.2x16.1	yel. " 2
26	" " 9	2.71	16.6x16.9x16.1	red, " 2
27	" " 8	2.68	16.4x16.9x16.	" " 2
28	" " 12	2.42	15.7x16.5x15.4	" " 2
29	" " 4	2.31	16.5x15.4x15.3	" " 2
30	" " 7	2.23	14.9x16.1x14.6	" " 2
31	" " 5	1.85	14. x14.6x13.2	" " 2
32	15-11-2. plant 5	4.51	24.5x18.9x18.1	" plum 2
33	" " 7	3.53	19. x18.7x17.7	yel. sph. 2
34	" " 1	2.72	17. x16.8x16.1	" " 2
35	" " 3	1.47	17.3x15.9x15.8	red, " 2
36	" " 6	2.33	16.8x15.9x15.4	" " 2
37	17-12-4. " 1	2.52	20.2x15.8x15.4	" egg, 2
38	" " 6	1.51	16.1x16.4x16.2	yel. sph. 2
39	" " 8	2.38	16.4x16.3x15.6	red, " 2
40	" " 10	1.90	15. x14.5x14.	" " 2
41	" " 7	1.22	14.3x13. x12.5	" " 2
42	max. 7-11-2. " 4	1.04	12. x12.7x12.	" " 2
42	av. " " 4	.73	11.2x11. x19.4	" " 2
42	min. " " 4	.10	5.2x5. 7x 5.5	" " 2

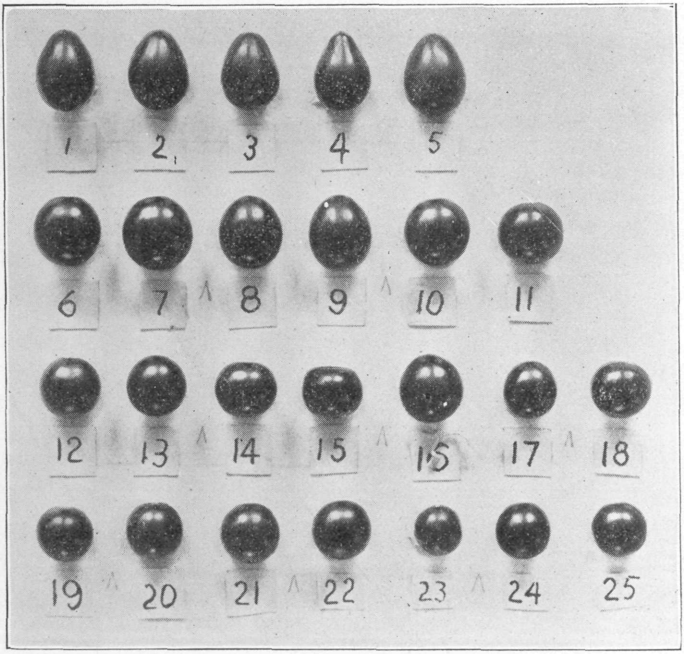
PLATE XXIV.

These fruits, harvested on September 24, 1914, were photographed on the following day. Two fruits were taken from each plant. In addition to the data given below, the number of seeds of each fruit has been recorded. The identity of the fruits is as follows :

NO. OF FRUITS.	FRUIT TAKEN FROM	WEIGHT IN GRAMS.	POLAR LENGTH, MAX. DIAMETER, MIN. DIAMETER.	COLOR, SHAPE AND NO. OF LOCULES.
1	43-14-2. plant 2	2.96	21.4x15.5x15.3	yel. egg, 2
2	" " 2	2.76	21. x15.8x15.	" " 2
3	" " 2	2.70	20.7x15.9x15.5	" egg-pear 3
4	" " 2	2.24	20.9x15. x14.2	" pear 2
5	" " 2	3.02	21.9x16.6x15.3	" egg 2
6	" " 7	3.08	18.3x17.5x16.2	red, sph. 2
7	" " 7	3.39	19.1x18.2x16.3	" " 2
8	" " 11	2.93	19.3x16.9x16.	" plum 2
9	" " 11	2.93	20.1x16.8x15.9	" " 2
10	" " 10	2.77	17.3x16.8x15.5	yel. sph. 2
11	" " 10	2.66	15.9x17. x15.8	" " 3
12	" " 9	2.33	15.6x15.6x15.	red " 2
13	" " 9	2.23	15.5x15.3x14.7	" " 2
14	" " 1	1.33	14.5x16.1x15.6	yel. " 3
15	" " 1	2.31	x15.8x	" " 3
16	" " 8	2.88	17.8x17. x16.7	red " 3
17	" " 8	1.72	14.9x13.9x13.5	" " 2
18	" " 4	2.21	15. x15.8x14.8	" " 2
19	" " 4	1.95	14.5x15. x14.6	" " 3
20	" " 3	2.23	15.7x x14.6	yel. " 2
21	" " 3	2.13	15.6x15.5x14.7	" " 2
22	" " 5	2.17	15.1x14.8x14.1	red " 2
23	" " 5	1.44	x x	" " 2
24	" " 6	1.77	14.8x14.2x13.6	" " 2
25	" " 6	1.72	14.4x14.4x13.3	" " 2



PERRY on "Inheritance of Size in Tomatoes."



PERRY on "Inheritance of Size in Tomatoes."